

Cryptic diversity and phylogeography of high alpine *Sattleria*—a case study combining DNA barcodes and morphology (Lepidoptera: Gelechiidae)

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Abstract

The taxonomy of *Sattleria*, a genus restricted to European high mountain systems, is critically revised based on morphology, DNA barcodes and phylogeography. Adult morphology combined with sequence information for the barcode region of COI supports the existence of 14 species. The full 658bp fragment of COI was obtained from 43 specimens representing 11 species and three shorter sequences were obtained from another two species. An illustrated key to the male genitalia of all species is provided. Three new species are described: *Sattleria karsholti* **sp. nov.** (Alpi Orobie, Adamello and Monte Baldo, Prov. Bergamo, Trento and Verona, Italy), *Sattleria cottiella* **sp. nov.** (Cottian Alps, Prov. Cuneo, Italy), and *Sattleria graiaaeella* **sp. nov.** (Alpi Graie, Prov. Aosta, Italy; Savoie, France). *Sattleria basistrigella* Huemer, 1997 **bona sp., stat. rev.** is raised from subspecies rank of *Sattleria triglavica* Povolný, 1987 to species rank.

Key words: Lepidoptera, Gelechiidae, *Sattleria*, phylogeography, cryptic diversity, new species, revised status, barcode, morphology, Europe, high mountains

Introduction

Lepidoptera from the Alps have recently gained increasing attention resulting in the description of numerous new, mostly endemic taxa (Huemer 1998, 2011). Several of these new taxa belong to hitherto unrecognized species complexes, many with brachypterous, flightless females which are well adapted to alpine environments (Sattler 1991, Whitebread 2007). The genus *Sattleria*, described by Povolný (1965), provides a striking example of such overlooked alpha-diversity. Although the first species was described in the 19th Century (Nowicki 1864), only two further species were known until recently. During the last two decades of the 20th Century several new species were described, mainly based on morphological characters of the adults and their genitalia. Some of these taxa occurred sympatrically, strongly supporting their status as distinct species (Huemer and Sattler 1992, Pitkin and Sattler 1991). However, Povolný (1987, 2001) argued that intraspecific variation was exceptionally high and only recognized a single highly polymorphic species, viz. *Sattleria dzieduszyckii* (Nowicki, 1864), separated into five subspecies (Povolný 2002). These conflicting taxonomic treatments were reviewed by Huemer and Karsholt (2010) who defined 10 species of *Sattleria* based on morphological characters and partially supported by a preliminary molecular dataset for a few taxa. Since this time, we have tried to advance species concepts in the genus through integrative taxonomy (Schlick-Steiner *et al.* 2010) including the acquisition of DNA barcodes from representative voucher specimens of *Sattleria*. These studies revealed considerable interspecific sequence divergence supporting the validity of the species recognized through prior morphological study. However, this work also revealed a surprising level of genetic diversity, particularly in the southwestern Alps, an observation that provoked our decision to revise the genus combining molecular and morphological traits.

Material and methods

New and newly revised species are described in detail, whereas descriptions and diagnoses of other taxa may be obtained from extensive earlier reviews e.g. Microlepidoptera of Europe volume 6 (Huemer and Karsholt 2010). Diagnostic features in females are not considered due to the lack of representative specimens for all newly described species.

We examined 270 dried, pinned and partially set specimens. Genitalia preparation followed standardized techniques (Robinson 1976) adapted for Gelechiidae and using by adoption of the unrolling technique (e.g. Pitkin and Sattler 1991).

Wingspan is defined as the distance between the forewing apices of set specimens. Because accurate measurement is sometimes difficult or impossible to make, particularly in worn, unset or badly set material, the scale unit is only in half millimeters.

Photographs of the adults were taken through an Olympus SZX 10 binocular microscope and Olympus E 3 digital camera and processed with Helicon Focus 4.3 software and using Adobe Photoshop and Lightroom 2.3. Genitalia were photographed with an Olympus E1 digital camera through an Olympus BH2 microscope.

Maps are based on examined material exclusively and were produced with the software program BIOOFFICE.

65 specimens of *Sattleria* were sequenced at the Canadian Centre for DNA Barcoding (CCDB, Guelph) to obtain DNA barcodes (COI 5' fragment of 658 bp) using the standard high-throughput protocol as described in Ivanova *et al.* (2006), resulting in a full barcode fragment for 43 specimens (11 species) and shorter sequences for 8 specimens (including two additional species). No suitable material was available for *S. angustispina*. Details on the voucher specimens can be obtained from the public project "PHLAS - Lepidoptera of the Alps - *Sattleria*" in the Barcode of Life Data Systems (BOLD; Ratnasingham and Hebert 2007). Barcode sequences were submitted to GenBank and have the following accession numbers: GU689182, GU689218, HM381543, HM381545, HM381572, HM381612, HM381613, HM381633, HM381638, HM426025, HM426026, HM432292, HM910632, HM910633, HQ968320, HQ968595, HQ968624, HQ968625, HQ968634, HQ968635, HQ968643, HQ968660–HQ968664, HQ968744, HQ968745, HQ968951, HQ968952–HQ968955, HQ968960–HQ968965, JF860407, JN200802–JN200812.

Sequence divergences were quantified using the Kimura 2-parameter model implemented within the analytical tools on BOLD.

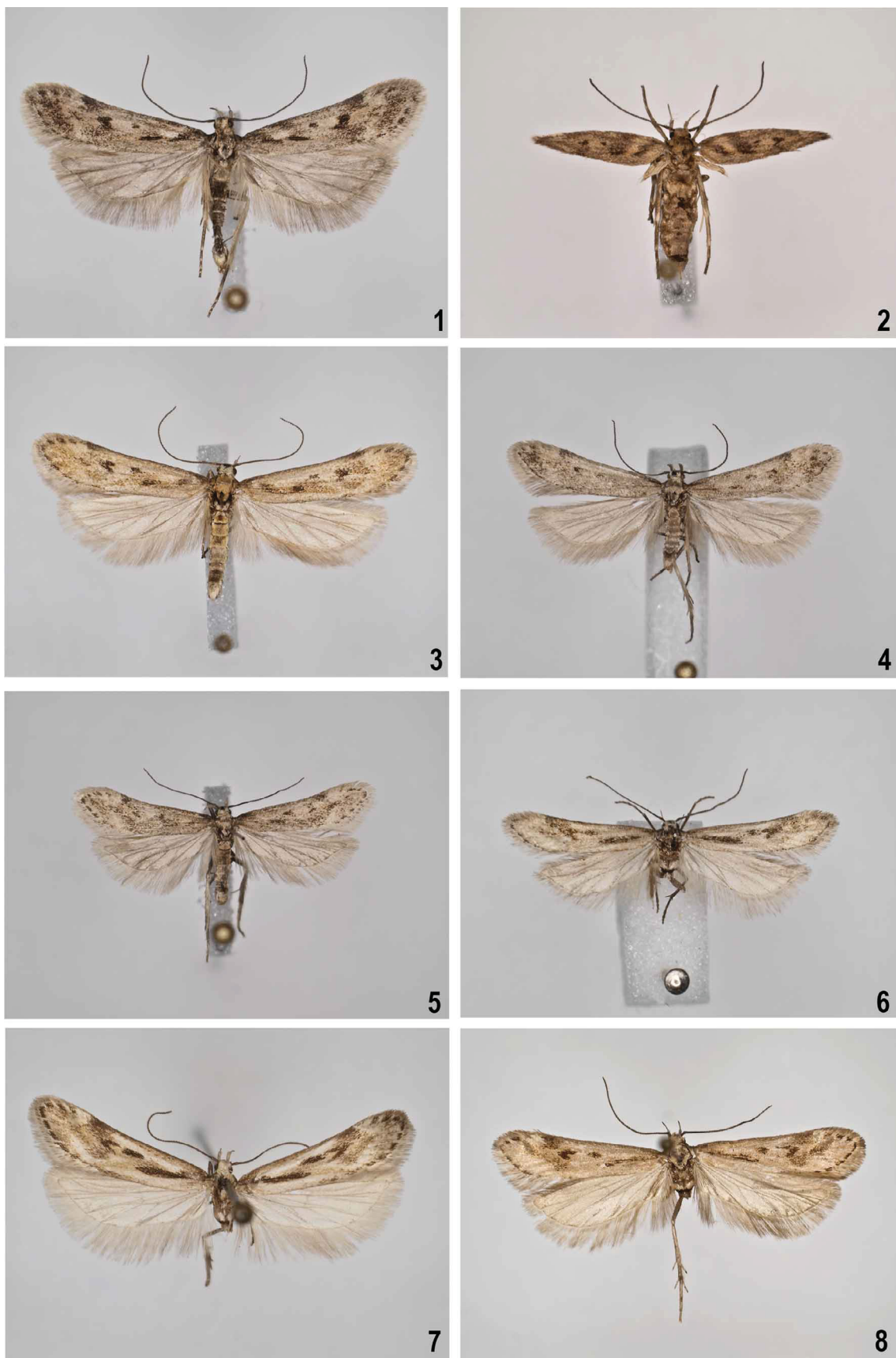
The following abbreviations are used for institutions and private collections: LMK—Landesmuseum Kärnten, Klagenfurt, Austria; LNK—Staatliche Sammlungen für Naturkunde, Karlsruhe, Austria; NHMW—Naturhistorisches Museum, Vienna, Austria; RCGB—Research collection Giorgio Baldizzone, Asti, Italy; RCNP—Research collection Norbert Pöll, Bad Ischl, Austria; RCTG—Research collection Theo Grünewald, Landshut, Germany; RCTM—Research collection Toni Mayr, Feldkirch, Austria; TLMF—Tiroler Landesmuseum Ferdinandeum, Innsbruck, Austria; ZMUC—Zoological Museum, Natural History Museum of Denmark, Copenhagen, Denmark; ZSM—Zoologische Staatssammlung, Munich, Germany.

Results

Genus *Sattleria* Povolný, 1965

Type species: *Gelechia dzieduszyckii* Nowicki, 1864 by monotypy and original designation.

Diagnosis. Adult (Figs 1–8). Head smoothly scaled, labial palpus recurved, second segment with short brush of scales ventrally, third segment acute, about length of second segment. Wingspan ♂ 15–24 mm, ♀ 10–19 mm. Male with longish forewing, maximum width at about 4/5; hindwing broad. Female with short and distinctly pointed forewing, maximum width in basal third; hindwing largely reduced, short and pointed flap of about 1/3 length of forewing. Forewings of both sexes light grey brown to mid-brown, frequently with darker mottling in basal third and at about 2/3; dark brown markings consisting of basal streak or one to two elongate black stigmata in fold and further spots at middle and end of cell, the latter frequently angulated; termen often with black dots, particularly in male. Hindwings light grey.

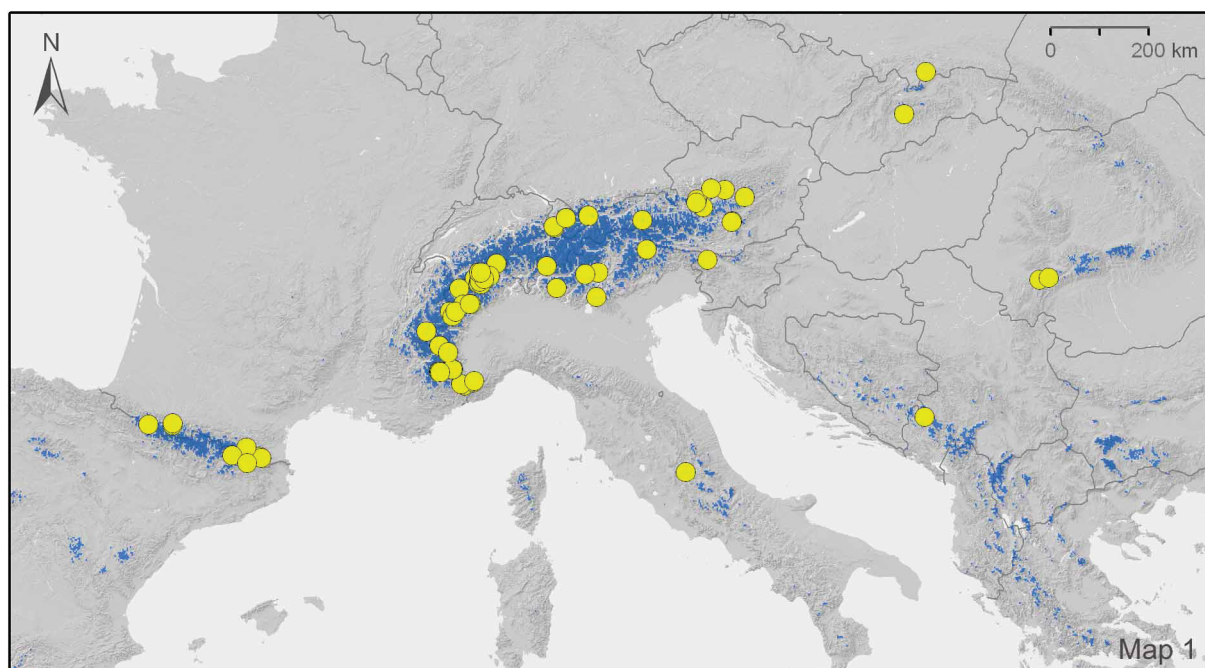


FIGURES 1–8. Adults of *Sattleria*. 1–2, *S. melalecuella* (Constant), 1, ♂, 2, ♀; 3, *S. karsholti* **sp. nov.**, ♂, holotype; 4, *S. cot-tiella* **sp. nov.**, ♂, holotype; 5, *S. izoardi* Huemer & Sattler, ♂; 6, *S. graiaeella* **sp. nov.**, ♂, holotype; 7, *S. basistrigella* Huemer, ♂; 8, *S. triglavica* Povolný, ♂.

Male genitalia (Figs 9–35). Subgenital segments: sternite VIII sub-oval, with or without weak emargination medially; tergite VIII tongue-shaped, slender; uncus short and moderately slender, with rounded apex; gnathos hook strong, culcitula distinct; tegumen gradually widened from uncus to pedunculi, anterior margin deeply emarginate; pedunculi long, slender; valva long, slender, straight to weakly curved; saccus shorter than valva, distally pointed, basal part with or without rounded lobe; vinculum broad, deeply emarginate posteriomedially with pair of long, strongly sclerotized, needle-shaped to forked processes, occasionally with lateral lobe; saccus about length to slightly shorter than processes, broad with almost parallel margins and rounded to cut-off apex; anellus with pair of small, rounded, centrally perforated sclerites; phallus long, slender, straight to weakly curved, coecum weakly separate, apex with sclerotized plate and short arm, ventromedial part occasionally with projection.

Female genitalia (see Huemer and Karsholt 2010). Apophysis posterioris very long; sternum VIII strongly sclerotized, with pair of small and drop-like pockets; sternite VIII medially with irregular folds or ridges; apophysis anterioris about length of segment VIII, about one-third length of apophysis posterioris, basally strongly sclerotized and extended into ostium bursae and to sternal pockets; antrum long and tubular; ductus bursae about length of or shorter than antrum; corpus bursae spherical to oval, usually without, rarely with barely discernible signum.

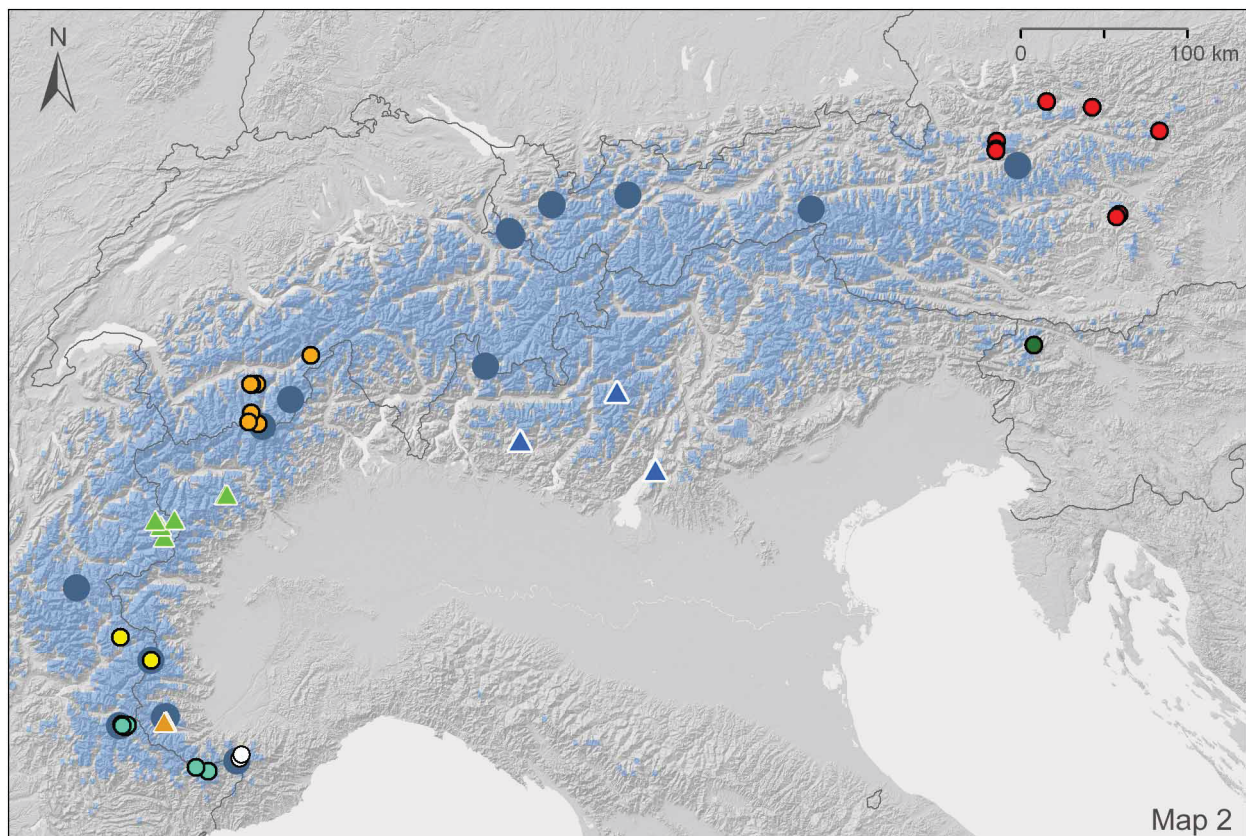
Bionomics. The biology of most species of *Sattleria* is insufficiently described and only a few authors such as Burmann (1954) deal with the habits of preimaginal stages. The ovum and oviposition sites are unknown. The larval stages have been recorded from various Caryophyllaceae (*Silene* spp., *Moehringia* sp.) and Saxifragaceae (*Saxifraga* spp.). They have been found in July and August, feeding from a loosely spun silken tube that is often extended from the upper parts of the host-plant to the roots or nearby stones (Pitkin and Sattler 1991). Frass is deposited outside the larval tube. The simultaneous presence of different larval stages indicates a biennial phenology, but phenology may depend on the location and microclimatic conditions. Hibernation probably takes place in the larval stage. Early snowfall shortly after the flight season indicates an alternative hibernation of the pupa or the ovum (Huemer, pers. obs.). The larvae apparently pupate near the ground surface in a dense cocoon, often under stones or amongst the host-plant. Adults have been collected from late June and mid-September. Burmann (1954) observed a mating pair in the early afternoon, whereas Pitkin and Sattler (1991) suspected that increased male activity about midnight was related to their search for females at that time. According to personal observations (P.H.) the males of two species were found in large numbers and extremely active in the early morning at temperatures slightly above zero, indicating mating behaviour. Males of most if not all species are easily attracted to different artificial light sources. Species of *Sattleria* are restricted to alpine habitats such as scree and rock formations with sparse vegetation as well as alpine grassland, preferably on calcareous, rarely on siliceous soil. The vertical distribution ranges from about 2000 to 3500 m, exceptionally as low as 1500 m.



MAP 1. The distribution of the genus *Sattleria* in Europe (exclusively based on examined material); altitudinal zones above 1600 m s.l. in blue.

Distribution. Species of *Sattleria* are restricted to the European mountain systems (Map 1). They have been recorded mainly from the Alps where diversity reaches its highest level with 10 species (Map 2). The genus is also represented in the Pyrénées by three additional species—*S. arcuata* Pitkin & Sattler, 1991, *S. pyrenaica* (Petry, 1904), and *S. angustispina* Pitkin & Sattler, 1991. The Carpathian Mountains are inhabited by a single endemic species, *S. dzieduszyckii* (Nowicki, 1864) whereas the Dinaric Mountains and the Apennines share their single species with the Alps (*S. triglavica* Povolný, 1987 and *S. melaleucella* (Constant, 1865) respectively). A record from the Balkan Mountains is dubious and whereabouts of the material are unknown (Pitkin & Sattler 1991). No records of *Sattleria* are known from the Caucasus or Mediterranean mountain systems.

Remarks. The external and genitalia morphology for most taxa have been extensively described by Pitkin and Sattler (1991), Povolný (1987, 2001, 2002) and most recently Huemer and Karsholt (2010), and particularly the last mentioned revision may be used as a reference. Descriptions in this publication are restricted to new and revised taxa and because of the absence of females the latter are necessarily omitted from diagnoses.



Sattleria

- | | |
|-----------------------------------|--------------------------------------|
| ● melaleucella (Constant, 1865) | ● breviramus Pitkin & Sattler, 1991 |
| ▲ cottiella Huemer & Hebert, 2011 | ● izoardi Huemer & Sattler, 1992 |
| ▲ graiaella Huemer & Hebert, 2011 | ○ marguareisi Huemer & Sattler, 1992 |
| ▲ karsholti Huemer & Hebert, 2011 | ● styriaca Pitkin & Sattler, 1991 |
| ● basistrigella Huemer, 1997 | ● triglavica Povolný, 1987 |

MAP 2. The distribution of taxa of the *Sattleria* in the Alps (exclusively based on examined material); altitudinal zones above 1600 m s.l. in blue.

Checklist of *Sattleria* species

Sattleria Povolný, 1965

Sattleria melaleucella (Constant, 1865)

= *Gelechia mariae* Frey, 1867 unavailable, infrasubspecific

= *Gelechia dzieduszyckii fusca* Burmann, 1954

Sattleria arcuata Pitkin & Sattler, 1991

Sattleria pyrenaica (Petry, 1904)

Sattleria karsholti Huemer & Hebert, 2011 **sp. nov.**

Sattleria cottiella Huemer & Hebert, 2011 **sp. nov.**

Sattleria marguareisi Huemer & Sattler, 1992

Sattleria izoardi Huemer & Sattler, 1992

Sattleria graiaaeella Huemer & Hebert, 2011 **sp. nov.**

Sattleria dzieduszyckii (Nowicki, 1864)

= *Gelechia dzieduszyckii tatrica* Gregor & Povolný, 1955

Sattleria triglavica Povolný, 1987

Sattleria basistrigella Huemer, 1997 **bona sp., stat. rev.**

= *Gelechia dzieduszyckii* [sic] f. *basistrigella* Müller-Rutz, 1934 unavailable, infrasubspecific

Sattleria angustispina Pitkin & Sattler, 1991

Sattleria breviramus Pitkin & Sattler, 1991

Sattleria styriaca Pitkin & Sattler, 1991

Illustrated key to the species of *Sattleria*

Note. The key is solely based on male genitalia characters. Further supplementing data including figures of external characters are available in Huemer and Karsholt (2010).

- 1 Sacculus evenly tapered to pointed apex, or medially broadened with short and slender apical part; secondary process of vinculum arising from basal third or middle of primary process (Figs 9–20) 2
- Sacculus with broad and hump-like base, distal part abruptly tapered; secondary process of vinculum arising at base of primary process or absent (Figs 21–23) 12
- 2 Secondary process of vinculum with pointed apex (Figs 9–15, 24–31) 3
- Secondary process of vinculum broadly rounded (Figs 16–20, 32–35) 8
- 3 Vincular processes separated into long primary and short, spine-shaped secondary process (Figs 9–12, 24–27) 4
- Vincular processes forked, separated into needle shaped primary and long and slender secondary process (Figs 13–15, 28–31) 6
- 4 Primary process of vinculum serrated (Fig. 11) *S. arcuata*
- Primary process of vinculum without serration (Figs 9–10, 12) 5
- 5 Phallus with long medial process; secondary process of vinculum a slender spine (Figs 9–10, 26–27) *S. melaleucella*
- Phallus with indistinct medial process; secondary process of vinculum a broadly based spine (Figs 12, 24–25) *S. karsholti* **sp. nov.**
- 6 Secondary process of vinculum about length of distal part of primary process, arising at right angle (Fig. 13) *S. pyrenaica*
- Secondary process of vinculum distinctly shorter than distal part of primary process, arising at acute angle (Figs 14–15, 28–31) 7
- 7 Secondary process of vinculum arising at angle of about 60°, less than one-half length of distal part of primary process (Figs 14, 28–29) *S. cottiella* **sp. nov.**
- Secondary process of vinculum arising at angle of about 30°, about two-thirds length of distal part of primary process (Figs 15, 30–31) *S. izoardi*
- 8 Sacculus evenly tapered; phallus with long and curved sclerotized arm near apex (Figs 16, 18) 9
- Sacculus medially broadened; phallus with short and straight sclerotized arm near apex (Figs 17, 19–20) 10
- 9 Secondary process of vinculum arising in middle of primary process, hump-like (Fig. 16) *S. marguareisi*
- Secondary process of vinculum arising near base of primary process, shape of a shark's fin (Fig. 18) *S. dzieduszyckii*
- 10 Phallus with distinct medial process (Fig. 17) *S. graiaaeella* **sp. nov.**
- Phallus without medial process (Figs 19–20) 11
- 11 Secondary process of vinculum broad, evenly convex (Figs 19, 35) *S. triglavica*
- Secondary process of vinculum small, posterior margin concave (Figs 20, 34) *S. basistrigella*
- 12 Secondary process of vinculum absent (Fig. 21) *S. breviramus*

- Secondary process of vinculum distinct, spine-shaped (Figs 22–23) 13
- 13 Sacculus with long and straight distal part, basal part broadly convex; secondary process of vinculum slender, needle-shaped to tooth-like (Fig. 23) *angustispina*
- Sacculus with moderately long and curved distal part, basal part with distinct hump; secondary process of vinculum distinctly broader at base, distal part slender, tooth-like (Fig. 22) *S. styriaca*

New and revised taxa

Sattleria karsholti sp. nov.

(Figs 3, 12, 24–25)

Type material. Holotype ♂, 'Italia sept. Prov. Bergamo Alpi Orobie Val d'Arera 2100 m 14.-15.8.1992 leg. Hue-mer' 'BC TLMF Lep 1439' (TLMF).

Paratypes. Italy: 1 ♂, same data as holotype, gen. slide GEL 1132 (TLMF); 7 ♂, Prov. Trento, Adamello, Mandron, 2800 m, 30.7.-1.8.1964, leg. Burmann, gen. slides GEL 131, LMP 52, LMP 71 (LNK; TLMF; ZMUC); 2 ♂, same data, but end 7.1967, leg. Burmann; 1 ♂, same data, but 2700 m, mid 8.1958, leg. Burmann, gen. slide LMP 89 (LNK); 1 ♂, same data, but 2500 m, 15.8.1985, leg. Schütz (RCTG); 1 ♂, same data, but 2600 m, 15.8.1989, leg. Schütz (RCTG); 1 ♂, Prov. Verona, Monte Baldo, Telegrafo, 2150 m, mid 7.1969, leg. Burmann, gen. slide LMP 74 (LNK); 1 ♂, Prov. Verona, Monte Baldo, Cima Valdritta, 2200 m, 15.7.1987, leg. Huemer & Tarmann, gen. slide GEL 162 (TLMF); 1 ♂, Prov. Verona, Monte Baldo, Longino, 2200 m, 29.6.1985, leg. Tar-mann (TLMF).

Description. Adult (Fig. 3). Head cream-coloured, rarely mid-brown, labial palpus cream-coloured, with few mid-brown scales on outer surface, tip of segment three brownish; antenna blackish brown; thorax and abdomen mid-brown, mixed with some rusty brown. Wingspan ♂ 17.5–20.5.0 mm; forewing ground colour underlies some variation, from light creamy brown to darker grey-brown, rusty brown along subcosta, fold and in basal half of forewing, medial part of wing intensively mottled cream, indistinct angulate cream fascia at 4/5 inwardly bordered by irregular transverse dark brown fascia; black markings: dash in fold, subcostal spot at 2/5 and angulated spot at 3/5 in middle of forewing, furthermore some black mottling at base and along costa, termen with black dots; fringes concolorous with ground colour, weakly defined fringe line present; hindwing light grey with concolorous fringes. Female unknown.

Male genitalia (Figs 12, 24–25). Uncus with evenly rounded apex; gnathos hook strong, culcitula large; tegu-men anteriorly widened, broadly and deeply emarginated anterior margin; pedunculi long, slender; valva long, slender, extending almost to apex of uncus, nearly straight; sacculus shorter than valva, evenly tapered to apical point, basally without lobe; vinculum deeply emarginated with pair of long processes; primary process long and broadly digitate, distal half with few fine setae, apically weakly narrowing, almost level with apex of sacculus; sec-ondary process short, sub-triangular spine, arising at right angle in basal third of primary process; saccus slightly shorter than primary vincular process, slender sub-rectangular with cut-off apex; anellus with pair of small, rounded, centrally perforated sclerites; phallus slender, nearly straight, with small medial projection, coecum weakly inflated, apex with short and straight sclerotized arm.

Female genitalia. Unknown.

Diagnosis. *Sattleria karsholti* sp. nov. is externally very similar to other medium-sized species of the genus, particularly to the south-western alpine population of *S. melaleucella*. However, *S. melaleucella* has a longer and more slender primary process of the vinculum, a longer spine-like secondary process and a large medial projection of the phallus (Figs 9–10, 26–27). In the somewhat similar *S. arcuata*, the primary vincular process is needle-shaped and serrated (Fig. 11). Intraspecific divergence at COI is absent in the two specimens examined whereas interspecific divergence is 2.34% to the nearest neighbour *S. margareisi*. The minimum distance to the allegedly conspecific *S. melaleucella* is higher at 4.11%.

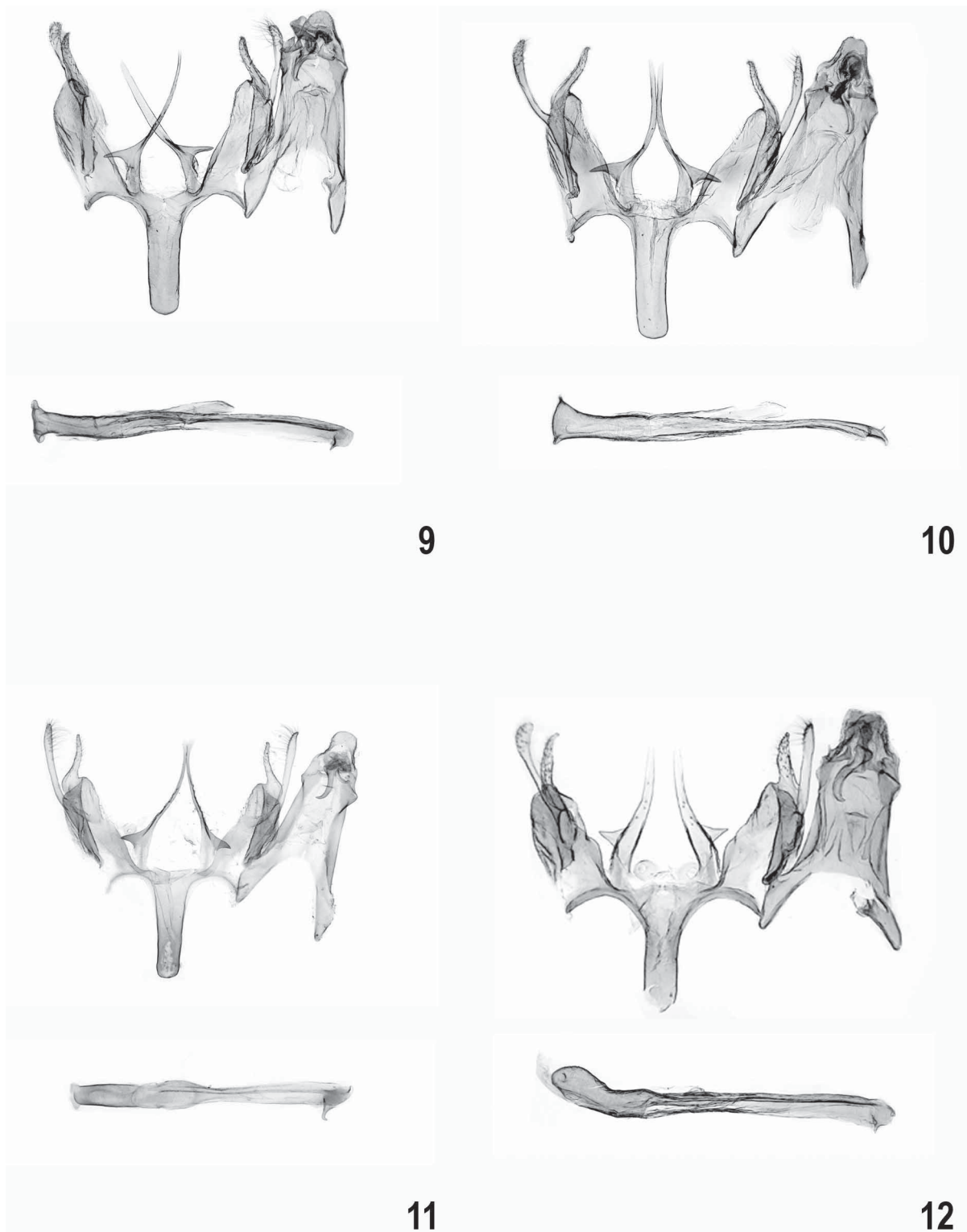
Bionomics. Host-plants and early stages are unknown. The adults have been collected from the end of June to mid-August. Habitats are alpine scree and rock formations primarily on limestone, but the species also occurs on siliceous soil with sparse vegetation at elevations ranging from about 2200 m to 2800 m.

Distribution. Only known from a small section of the southern Alps, ranging from Monte Baldo in the west to Pizo Arera in the east (Prov. Trento, Verona, Bergamo, Italy).

Etymology. The species is named after our colleague and friend Ole Karsholt (Zoological Museum, Copenhagen) in recognition of his outstanding contribution to European lepidopterology.

Remarks. *S. karsholti* **sp. nov.** was hitherto considered as the geographical form “C” of *S. melaleucella*, representing this species in the southern Alps (Pitkin and Sattler, 1991; see discussion). Despite the presence of several distinctive morphological characters, Pitkin and Sattler (1991) hesitated to introduce a new name in the absence of further evidence indicating species status.

Pl. 21, Fig. 207c in Huemer and Karsholt (2010) depicts *S. karsholti* **sp. nov.** and not *S. melaleucella*.



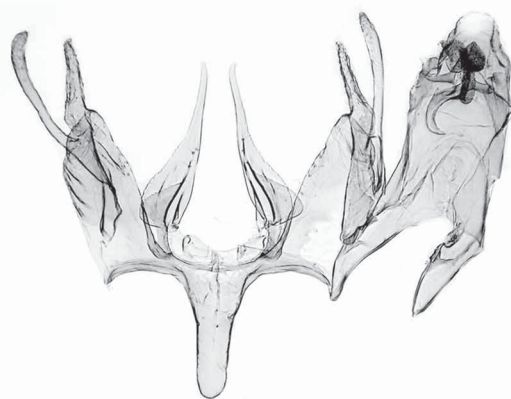
FIGURES 9–12. Male genitalia of *Sattleria*. 9, *S. melaleucella* (Constant), slide LMP 76; 10, *ditto*, slide LMP 102; 11, *S. arcuata* Pitkin & Sattler, paratype, slide GEL 159; 12, *S. karsholti* **sp. nov.**, paratype, slide LMP 71.



FIGURES 13–16. Male genitalia of *Sattleria*. 13, *S. pyrenaica* (Petty), slide GEL 279; 14, *S. cottiella* **sp. nov.**, paratype, slide GEL 1144; 15, *S. izoardi* Huemer, holotype, slide GEL 1145; 16, *S. marguareisi* Huemer & Sattler, paratype, slide GEL 150.



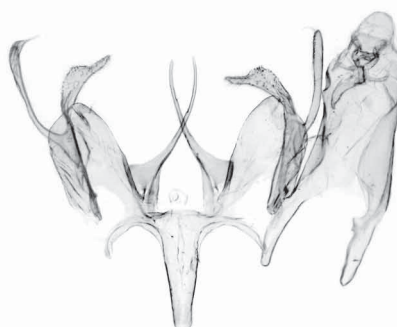
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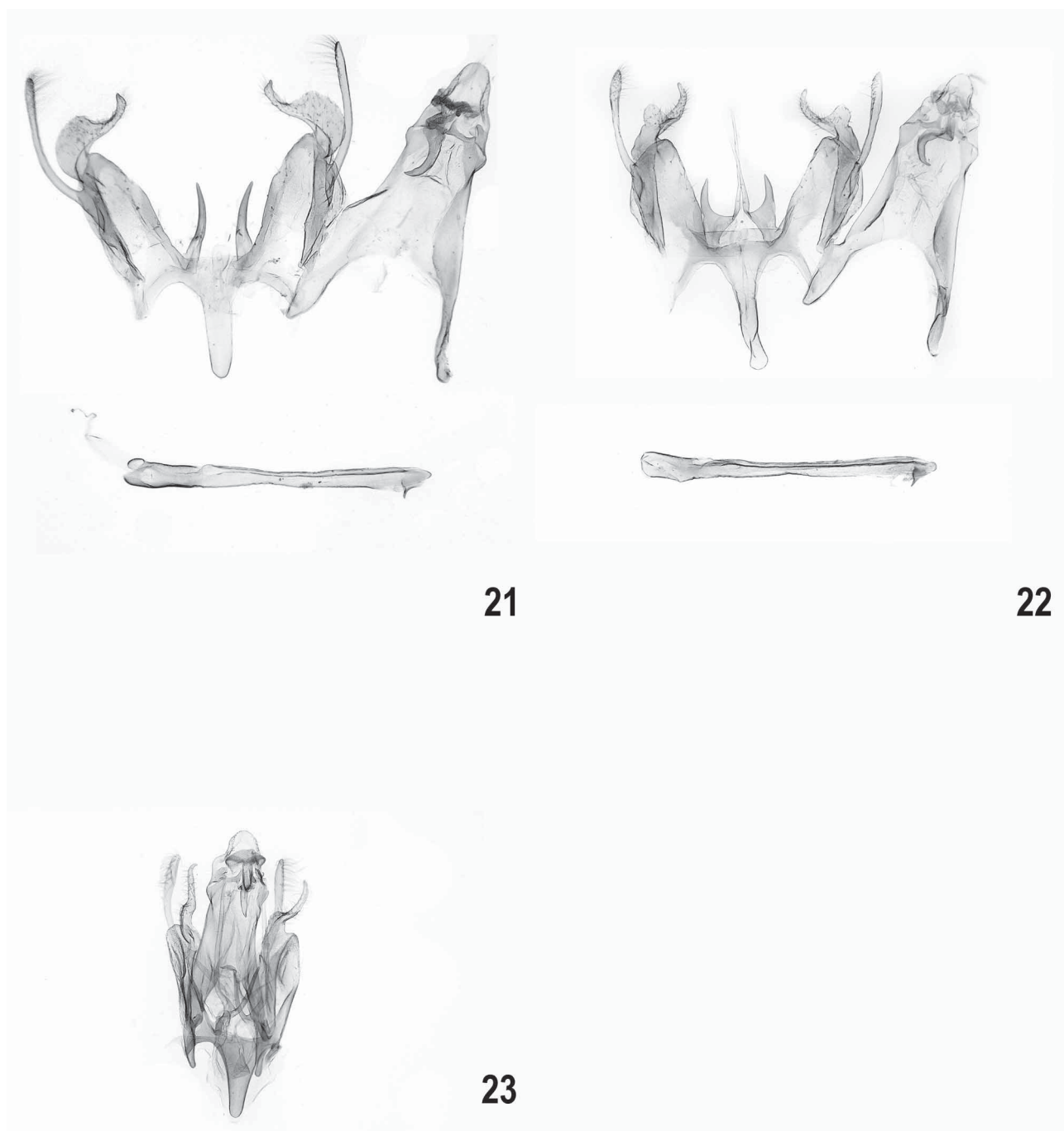


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FIGURES 17–20. Male genitalia of *Sattleria*. 17, *S. graiaaeella* **sp. nov.**, paratype, slide GEL 1135; 18, *S. dzieduszyckii* (Nowicki), slide Mus. Vind. 11242; 19, *S. triglavica* Povolný, paratype, slide Mus. Vind. 11241; 20, *S. basistrigella* Huemer, slide GEL 1139.



FIGURES 21–23. Male genitalia of *Sattleria*. 21, *S. breviramus* Pitkin & Sattler, slide GEL 154; 22, *S. stryriaca* Pitkin & Sattler, paratype, slide 91/230 P.H.; 23, *S. angustispina* Pitkin & Sattler, paratype, slide CG 84.

***Sattleria cottiella* sp. nov.**

(Figs 4, 14, 28–29)

Type material. Holotype ♂, 'Italien, Prov Cuneo Colle Valcavera 2420 m N 44°23,0' E 07°06,2' 27.7.2009 Mayr Toni leg.' (TLMF).

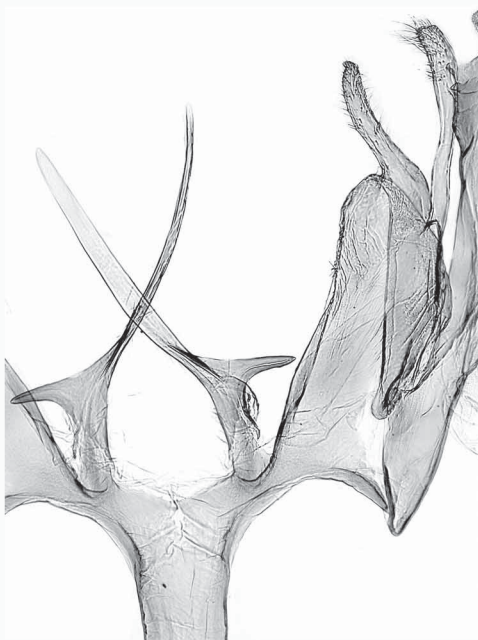
Paratypes. Italy: 5 ♂, same data as holotype (RCTM); 1 ♂, same data, but 4.8.2008, leg. Huemer (TLMF); 1 ♂, same data, but 23.7.2009, leg. Huemer (TLMF); 7 ♂, same data, but 2.8.2010, leg. Huemer (TLMF); 4 ♂, same data, but leg. Wieser (LMK); 13 ♂, Prov. Cuneo, Demonte NW, Colle Fauniera, 2480–2500 m, 3.8.2008, leg. Huemer, gen. slides GEL 1144, GEL 1146 (TLMF); 20 ♂, same data, but 28.7.2009, leg. Skou & Skule (ZMUC).



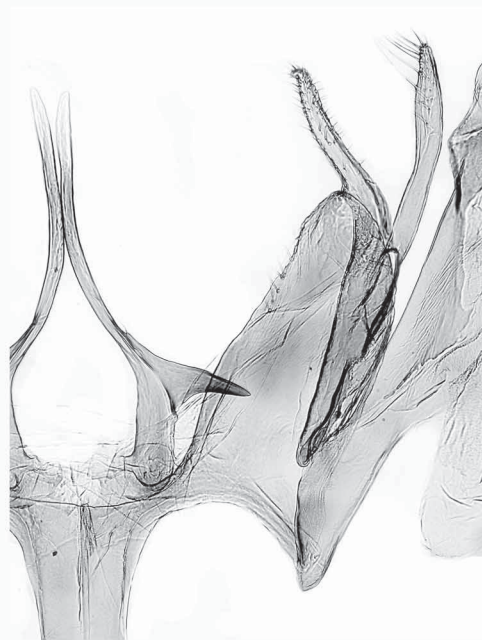
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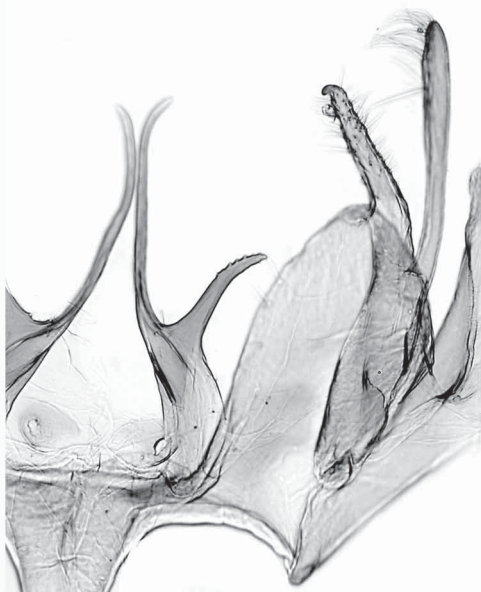


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FIGURES 24–27. Male genitalia of *Sattleria* (details of valva-vinculum complex). 24, *S. karsholti* **sp. nov.**, paratype, slide LMP 74; 25, *ditto*, paratype, slide LMP 71; 26, *S. melalecuella* (Constant), slide LMP 76; 27, *ditto*, slide LMP 102.



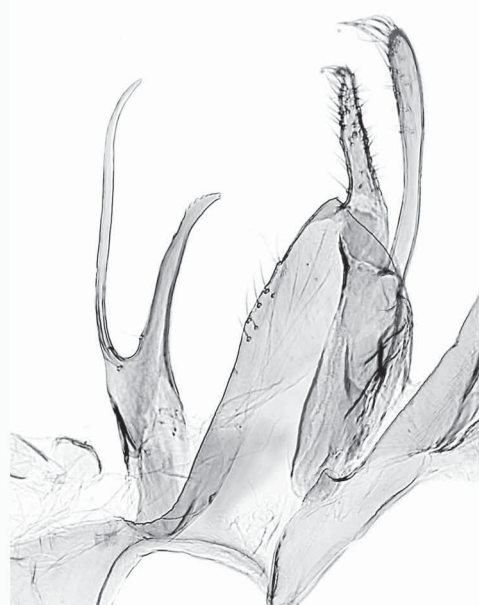
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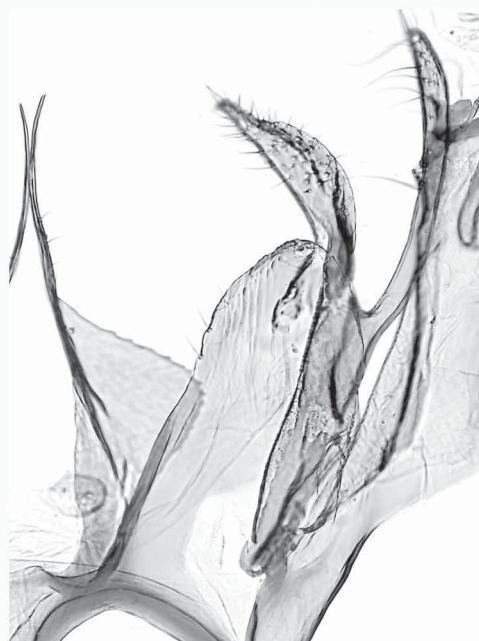


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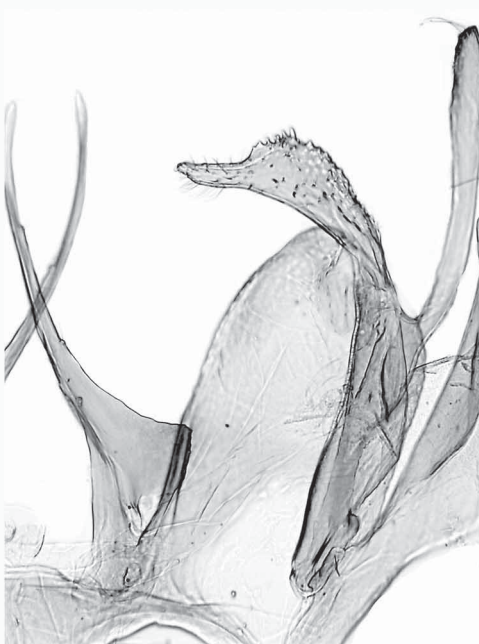
FIGURES 28–31. Male genitalia of *Sattleria* (details of valva-vinculum complex). 28, *S. cottiella* **sp. nov.**, paratype, slide GEL 1144; 29, *ditto*, paratype, slide GEL 1146; 30, *S. izoardi* Huemer & Sattler, holotype, slide GEL 1145; 31, *ditto*, slide GEL 1049.



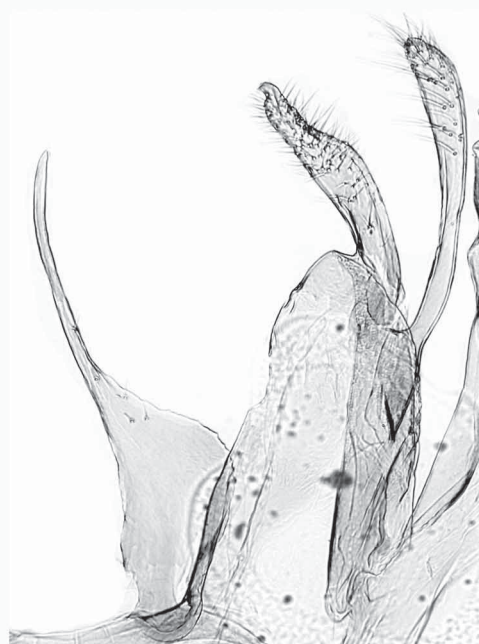
32



33



34



35

FIGURES 32–35. Male genitalia of *Sattleria* (details of valva-vinculum complex). 32, *S. graiaeella* **sp. nov.**, paratype, slide GEL 1135; 33, *ditto*, paratype, slide GEL 1136; 34, *S. basistrigella* Huemer, slide GEL 1139; 35, *S. triglavica* Povolný, paratype, slide Mus. Vind. 11202.

Description. Adult (Fig. 4). Head cream-coloured; labial palpus cream-coloured, with brown mottling on outer surface, tip of segment three darker brown; antenna blackish brown; thorax and abdomen light grey-brown, mixed with some rusty-brown. Wingspan ♂ 15.0–17.0 mm; forewing light brownish grey, rusty brown along fold and in medial part of the forewing, indistinct angulate light grey fascia at 4/5; black markings: dash in fold, subcostal spot at 2/5 and angulated spot at 3/5 in middle of forewing, furthermore some black mottling at base and along costa, termen with black dots; fringes concolorous with ground colour, weakly defined fringe line present; hindwing light grey with concolorous fringes. Female unknown.

Male genitalia (Figs 14, 28–29). Uncus with evenly rounded apex; gnathos hook strong, culcitula large; tegumen anteriorly widened, broadly and deeply emarginated anterior margin; pedunculi long, slender; valva long, slender, extending almost to apex of uncus, almost straight; sacculus shorter than valva, evenly tapered to apical point, basally without lobe; vinculum deeply emarginated with pair of long, forked processes; primary process basally broad, distal half needle-shaped, almost level with apex of sacculus; secondary process stiletto-shaped, about one-half length of distal half of primary process, arising at acute angle of about 60° from basal half of primary process, distal half with weakly serrated inner margin; saccus slightly shorter than primary vincular process, slender sub-rectangular with cut-off apex; anellus with pair of small, rounded, centrally perforated sclerites; phallus slender, nearly straight, without medial projection, coecum weakly inflated, apex with curved sclerotized arm.

Female genitalia. Unknown.

Diagnosis. *Sattleria cottiella* sp. nov. is externally very similar to other small species in the genus, particularly *S. izoardi*, *S. marguareisi* and *S. pyrenaica* which are on average smaller with 14.0–16.0 mm (*S. izoardi*), 15.0–16.0 mm (*S. marguareisi*) and 16.0 mm (*S. pyrenaica*) respectively. It differs from these taxa in its peculiar forked vincular processes: *S. pyrenaica* has a shorter and broader primary process and a broader secondary process which arises from the former at a right angle (Fig. 13); *S. izoardi* has a longer primary process and a distinctly longer secondary process of about 2/3 length of distal half of the former and arising from it at an acute angle of about 30° (Figs 15, 30–31); finally *S. marguareisi* differs in the unforked vincular processes replaced by a suboval secondary lobe (Fig. 16). Intraspecific divergence at COI is absent (n=5), whereas mean interspecific divergence is 1.91% to the nearest neighbour (*S. marguareisi*).

Bionomics. Host-plants and early stages are unknown. The adults have been collected from late July to early August in the first half of the night at light. Habitats are alpine scree and rock formations on limestone with sparse vegetation at elevations from about 2400 m to 2500 m.

Distribution. Only known from the southern part of the Cottian Alps (Prov. Cuneo, Italy), in a limited area in the surroundings of Colle Fauniera—Colle Valvacera.

Etymology. The specific name derives from the Ligurian prince Cottius, referring to the distribution area of this species, the Cottian Alps.

Remarks. *S. cottiella* sp. nov. was initially misidentified as *S. izoardi* on external appearance, but its status as a distinct species was first revealed by DNA barcoding and subsequently confirmed by detailed morphological analysis. Pl. 20, Fig. 205c in Huemer and Karsholt (2010) refers to the new species and has to be corrected accordingly.

Sattleria graiaeella sp. nov.

(Figs 6, 17, 32–33)

Type material. Holotype ♂, ‘Valle d’Aosta Champroucher Dondena sent. Mt. Rascias 2650 m ca. 21.VII.2006 G. Baldizzone leg.’ ‘G JN 20934 ♂ *Sattleria triglavica*’ ‘BC TLMF Lep 1083’ (TLMF).

Paratypes. Italy: 1 ♂, same data, but Dondena—Chila Desot, 2370–2450 m, 20.7.2006 (RCGB); 1 ♂, same data, but Dondena—Miserin, 2300–2450 m, 19.7.2006 (RCGB); 1 ♂, Prov. Aosta, Cogne, Lago di Loje, 2400 m, 8.7.1961, leg. Klimesch (ZSM); 4 ♂, Prov. Aosta, PN Gran Paradiso, Lago Serrù, 2275, 6.8.1992, leg. Delmastro, gen. slides GEL 1135, GEL 1136 (TLMF).

Excluded from the type-series: Material published by Pitkin and Sattler (1991) (see Remarks).

Description. Adult (Fig. 6). Head whitish cream, labial palpus whitish cream mottled with mid-brown; antenna blackish brown; thorax mid-brown, mottled with some whitish scales anteriorly, abdomen mid-brown. Wingspan ♂ 16.5–18.5 mm; forewing ground colour light cream-brown, intensively mottled whitish cream, mid-brown along costa; black markings well developed: broad black stripe through fold, angulated dash in middle of forewing at end

of cell and few black scales near base of forewing, termen with dark brown line; fringes concolorous with ground colour, weakly defined fringe line present; hindwing light grey with concolorous fringes. Female unknown.

Male genitalia (Figs 17, 32–33). Uncus with evenly rounded apex; gnathos hook strong, culcitula large; tegumen anteriorly widened, broadly and deeply emarginated anterior margin; pedunculi long, slender; valva long, slender, extending almost to apex of uncus, weakly curved; sacculus shorter than valva, medially broadened with slightly concave outer margin, abruptly tapered to short apical part; vinculum deeply emarginated with pair of processes; primary process long and needle-shaped, about level with apex of sacculus; secondary process arising from basal half of primary process, extremely broad based, outer edge broadly concave and serrated; saccus about length of primary vincular process, slender sub-rectangular with cut-off apex; anellus with pair of small, rounded, centrally perforated sclerites; phallus slender, nearly straight, with distinct medial projection, coecum scarcely inflated, apex with short and straight sclerotized arm.

Female genitalia. Not examined. It is likely that the female of the so-called south-western form of *S. basistrigella* from Savoie figured by Pitkin and Sattler (1991) in fact belongs to *S. graiaeella* **sp. nov.** (see Remarks).

Diagnosis. *Sattleria graiaeella* **sp. nov.** is externally similar to *S. basistrigella* and *S. triglavica* differing in the slightly smaller wingspan (16.5–18.5 mm versus 19.0–20.0 mm). However, the male genitalia of the new species are characterized by a distinct medial process of the phallus (Fig. 17) absent in the related species (Figs 19–20). The secondary process of the vinculum is large and almost evenly convex with serrated edge and thus distinct from both afore-mentioned taxa (Figs 32–35). The furthermore similar *S. dzieduszyckii* is distinguished by the evenly tapered sacculus and the different shape of the secondary vincular process (Fig. 18). No measure of intraspecific variation was possible as only a single individual was analyzed, but interspecific divergence was 2.98% to the nearest neighbour (*S. breviramus*). The minimal sequence distance to the allegedly conspecific *S. basistrigella* is 3.27%.

Bionomics. Host-plants and early stages are unknown. The adults have been collected from the end of June to mid-August. Habitats are alpine scree and rock formations primarily on limestone but also on siliceous soil with sparse vegetation at elevations ranging from about 2200 m to 2800 m.

Distribution. Only known from a small section of the western Alps, ranging from the Alpi Graie (Prov. Aosta, Italy) to Savoie (France).

Etymology. The species is named after the Roman province Alpes Graiae, the distribution area of the species.

Remarks. *S. graiaeella* **sp. nov.** was hitherto considered as a geographical form of *S. basistrigella* representing this species in the south-western Alps (Pitkin and Sattler 1991). The male genitalia figured by these authors leave no doubt about their conspecificity with the new species. We have not been able to examine this material which is therefore not included in the type-series. Particularly the females originating from a different locality than the males should be re-examined.

***Sattleria basistrigella* Huemer, 1997, bona sp., stat. rev.** (Figs 7, 20, 34)

Gelechia dzieduszykii [sic] f. *basistrigella* Müller-Rutz, 1934: 121, pl. 1, fig. 7; unavailable, infrasubspecific.

Sattleria triglavica basistrigella Huemer, 1997: 286, figs 1–2, 5.

Description. Adult (Fig. 7). Head cream, labial palpus cream, mottled with mid-brown; antenna blackish brown; thorax and abdomen mid-brown. Wingspan ♂ 19.0–20.0 mm; forewing ground colour light cream-brown, intensively mottled whitish cream, mid-brown along costa; irregular dark brown transverse band at 3/4; black markings well developed: broad black stripe through fold, angulated dash in middle of forewing at end of cell and few black scales near base of forewing, termen with several black spots; fringes concolorous with ground colour, weakly defined fringe line present; hindwing light grey with concolorous fringes. Female brachypterous (see Huemer and Karsholt 2010).

Male genitalia (Figs 20, 34). Uncus with evenly rounded apex; gnathos hook strong, culcitula moderate; tegumen anteriorly widened, broadly and deeply emarginated anterior margin; pedunculi long, slender; valva long, slender, shorter than uncus, weakly curved; sacculus shorter than valva, medially broadened with slightly concave outer margin, abruptly tapered to short apical part; vinculum deeply emarginated with pair of processes; primary process long and needle-shaped, about level with apex of sacculus; secondary process arising from basal half of

primary process, broad based, outer edge sub-rectangular, without serration; saccus shorter than primary vincular process, slender, sub-rectangular with cut-off apex; anellus with pair of small, rounded, centrally perforated sclerites; phallus slender, nearly straight, without medial projection, coecum scarcely inflated, apex with short and straight sclerotized arm.

Female genitalia. See Pitkin and Sattler (1991: fig. 59) and Huemer and Karsholt (2010).

Diagnosis. *Sattleria basistrigella* is externally similar to *S. graiaeella* **sp. nov.** and *S. triglavica* which were hitherto considered conspecific. It differs from the former by its larger wingspan (19.0–20.0 mm versus 16.5–18.5 mm) and from the latter in the more distinct transverse band of the forewing. Another similar species, *S. brevirmus*, differs in the black base of the forewing costa. Highly diagnostic characters are found in the male genitalia which differ from all related species particularly in the distinctly smaller and sub-rectangular secondary process of the vinculum (Figs 20, 34) which is large and convex in all other *Sattleria* species (Figs 17–19, 32–33, 35). The females of formerly mixed taxa are either unknown (*S. triglavica*) or their identity remains doubtful (*S. graiaeella* **sp. nov.**). The COI data indicate significant divergence with mean distances to other species of *Sattleria* ranging from a low of 2.98% (*S. brevirmus*) to 5.32%. The maximum intraspecific divergence detected was 0.85% (n=5).

Bionomics. The larva was observed in July feeding on *Silene acaulis* (L.) Jacqu., and living in a silken tube hidden inside cushions of the host-plant (Pitkin and Sattler 1991). The adults are on the wing from July to August, while laboratory-reared specimens emerged from late September to early October indicating plasticity in phenology. Habitats are alpine scree and rock formations primarily on siliceous soil with sparse vegetation at elevations ranging from about 2400 m to above 3000 m.

Distribution. Only known from the Pennine Alps in the southern part of the Valais (Switzerland). The single male record of this subspecies from the Italian Dolomites (Pitkin and Sattler 1991) was re-examined by us. It is based on a traditional male slide and important characters of the genitalia needed to confirm its identity are nearly invisible.

Remarks. Müller-Rutz (1934) introduced *basistrigella* as an infrasubspecific name and only recently the taxon was validated and formally re-described as *S. triglavica basistrigella* (Huemer 1997).

Molecular data

The full 658 bp barcode region was obtained from 43 of 65 voucher specimens and three additional sequences were >590bp. In addition, a 307 bp section of the barcode region was obtained from five specimens including the only two individuals of *S. arcuata*. Intraspecific divergence ranged from 0%–2.34% with a mean divergence of 0.84% (Tab. 1). Intraspecific divergences only exceeded 1% in two out of eight species while interspecific divergences ranged from 1.91–6.30% with a mean of 4.63% (Tab. 2).

TABLE 1. *Sattleria*: Intraspecific mean K2P (Kimura 2-Parameter) divergences and maximum pairwise distances based on the analysis of COI fragments (>500 bp).

	mean divergence	maximal distance	sample size
<i>S. melaleucella</i>	1.10%	1.87%	15
<i>S. pyrenaica</i>	-	-	1
<i>S. karsholti</i>	0.00%	0.00%	2
<i>S. cottiella</i>	0.00%	0.00%	5
<i>S. marguareisi</i>	0.00%	0.00%	3
<i>S. izoardi</i>	0.10%	0.15%	4
<i>S. graiaeella</i>	-	-	1
<i>S. dzieduszyckii</i>	-	-	1
<i>S. triglavica</i>	-	-	1
<i>S. basistrigella</i>	0.32%	0.85%	6
<i>S. brevirmus</i>	0.12%	0.31%	5
<i>S. styriaca</i>	2.34%	2.34%	2

TABLE 2. *Sattleria*: Interspecific mean K2P (Kimura 2-Parameter) divergences (mean pairwise distances) based on the analysis of COI fragments (>500 bp).

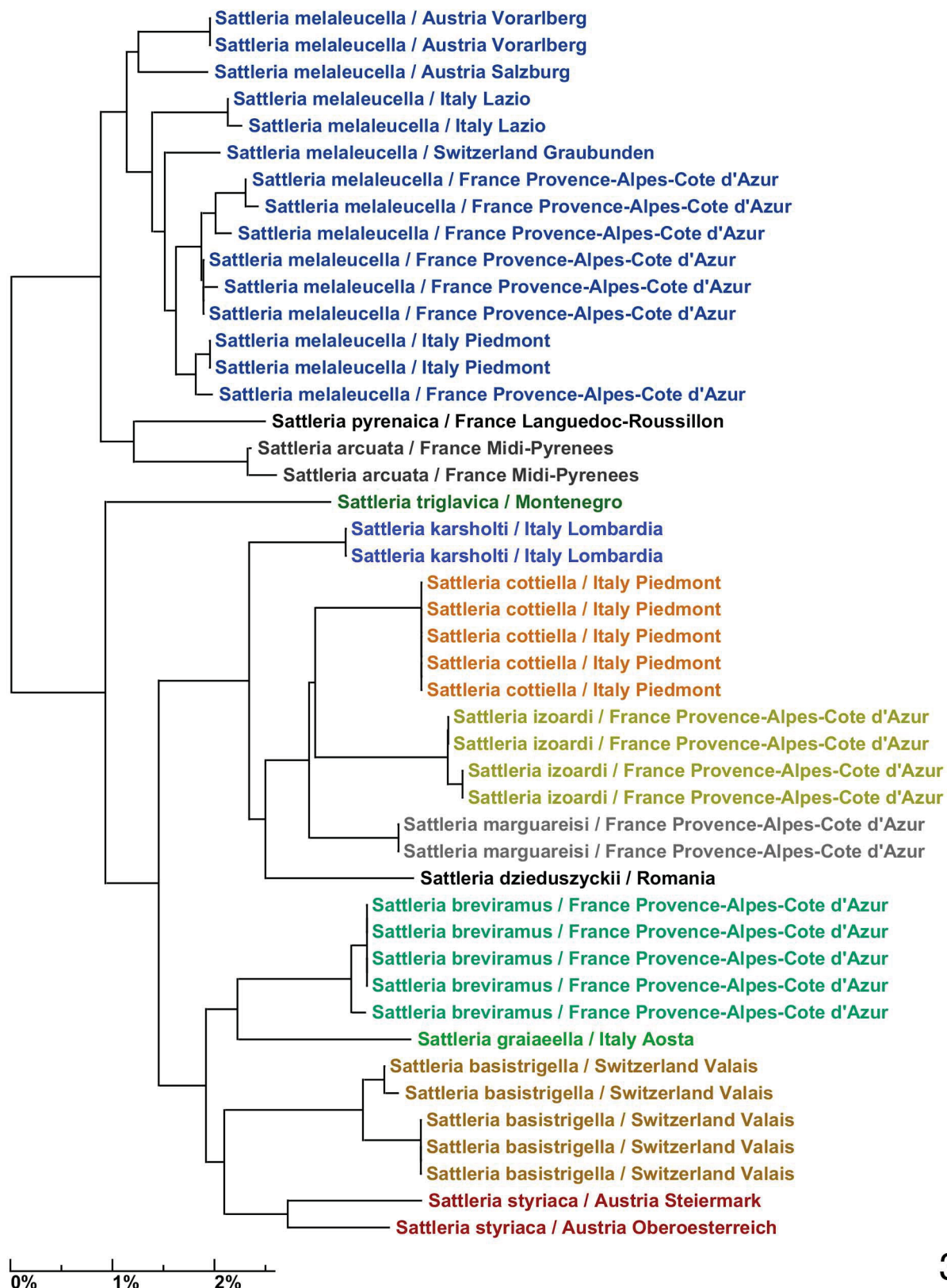
	<i>S. melaleucella</i>	<i>S. pyrenaica</i>	<i>S. karsholti</i>	<i>S. cottiella</i>	<i>S. marguareisi</i>	<i>S. izoardi</i>	<i>S. graiaeella</i>	<i>S. dzieduszyckii</i>	<i>S. triglavica</i>	<i>S. basistrigella</i>	<i>S. breviramus</i>	<i>S. styriaca</i>
<i>S. melaleucella</i>												
<i>S. pyrenaica</i>	4.67%											
<i>S. karsholti</i>	4.42%	4.95%										
<i>S. cottiella</i>	5.33%	5.63%	2.82%									
<i>S. marguareisi</i>	5.24%	5.20%	2.37%	1.99%								
<i>S. izoardi</i>	5.53%	4.87%	3.39%	2.42%	2.20%							
<i>S. graiaeella</i>	5.36%	5.96%	4.44%	5.28%	4.85%	6.22%						
<i>S. dzieduszyckii</i>	5.26%	5.77%	2.47%	2.81%	2.81%	3.41%	4.63%					
<i>S. triglavica</i>	4.31%	5.28%	4.93%	5.61%	5.77%	6.54%	4.45%	6.10%				
<i>S. basistrigella</i>	5.32%	5.27%	4.38%	4.19%	4.06%	4.81%	3.58%	4.52%	4.86%			
<i>S. breviramus</i>	4.74%	5.29%	4.11%	4.78%	4.15%	5.53%	2.98%	4.34%	3.96%	3.62%		
<i>S. styriaca</i>	5.12%	5.10%	4.67%	4.68%	4.39%	5.43%	4.28%	4.94%	4.94%	3.57%	3.63%	

Discussion

The taxonomy of *Sattleria* is one of the most controversial topics in alpine lepidopterology with past views ranging from a single widespread, highly polymorphic species (Povolný 2001, 2002) to 11 species with partially sympatric distributions (Huemer and Sattler 1992, Pitkin and Sattler 1991). Huemer and Karsholt (2010) accepted the latter conclusion basing species discrimination mainly on diagnostic characters of genitalia and partially on differences in external morphology of the adults in traits such as size and wing markings. The present DNA barcode results not only support the validity of species in that study, but suggest the existence of several cryptic species in *Sattleria*.

The genetic variation in *Sattleria* is divided into two main lineages, one including separate the widespread Alpine-Apenninic *S. melaleucella* and the Pyrenean *S. pyrenaica* and *S. arcuata* (based on a 307 bp fragment), and the other comprising the rest of the species (Fig. 36). The considerable interspecific divergence in *S. melaleucella* is remarkable, with a mean pairwise distance from 4.31% to 5.53% (Tab. 2) to other species with full-length barcodes. Moreover, all these taxa are well separated by male (and, where known, by female) genitalia features and partially by characters of the habitus. In the Alps *S. melaleucella* shares its habitats with at least 5 out of 10 species: *S. cottiella* **sp. nov.**, *S. marguareisi*, *S. izoardi*, *S. breviramus* and *S. basistrigella* and furthermore sympatric occurrence with *S. graiaeella* **sp. nov.** and *S. styriaca* seems possible from distribution patterns (Map 2). A similar situation has been documented from the Pyrénées for *S. pyrenaica* which flies together with *S. arcuata* at Pic du Midi de Bigorre (Hautes-Pyrénées, France) and *S. angustispina* at Mont Canigou (Pyrénées Orientales). The mean pairwise genetic distance between the former two species of 2.77% (although based on partial barcode sequences), supports morphological characters which are substantial enough to indicate species status (Pitkin and Sattler 1991).

The second major genetic lineage of *Sattleria* includes the majority of the taxa, with eight morphologically separated species from the Alps, *S. triglavica* from Montenegro and *S. dzieduszyckii* from the Carpathian Mountains (Fig. 36). All alpine taxa have limited distributions, occurring only in allopatry (Map 2). The south-western Alps are particularly rich in species with six regional or local endemics, whereas only one additional species occurs in the southern Alps and two in the eastern Alps. Genetic distances among these taxa are substantial with mean interspecific divergences ranging from 1.99% to 6.22% (Tab. 2). Distances are lowest between species pairs from the south-western and southern Alps with divergences roughly ranging from 2–3%. Results of our molecular analyses largely correspond with earlier morphologically based species concepts and support the specific status of all



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FIGURE 36. Neighbour joining tree of the *Sattleria* (Kimura 2 Parameter) based on sequences of the mtDNA COI gene (barcode fragment 5', 658 bp), except for *S. arcuata* (307 bp) and *S. dzieduszyckii* (623 bp).

formerly described taxa. Furthermore they provided evidence for three overlooked species: *S. cottiella* **sp. nov.**, *S. graiaeella* **sp. nov.** and *S. karsholti* **sp. nov.** Whereas the latter two had been suspected as possible species (Pitkin and Sattler 1991), the former was completely overlooked although it clearly differs from its relatives in genitalia characters. *S. karsholti* **sp. nov.** shows a particularly high mean divergence (4.22%) from *S. melaleucella*, the species with which it was formerly united (Pitkin and Sattler 1991). Similarly, the considerable mean pairwise distance (3.58%) between *S. graiaeella* **sp. nov.** and *S. basistrigella* combined with morphological traits clearly indicates two well separated species. The third species hitherto treated as conspecific with *S. basistrigella*, the morphologically weakly separated *S. triglavica*, is well separate in the barcode from these taxa by a mean pairwise distance of 6.54% and 4.86% respectively.

Despite the well supported species discrimination by both morphology and barcodes, several taxonomic questions remain unresolved. Intraspecific genetic divergences are usually low and range from 0.0% to < 1%, or divergence is insufficiently known due to the lack of enough material for barcoding. The few exceptions deserve more detailed investigation as they may involve further cases of cryptic diversity (Tab. 1). *S. melaleucella* includes several distinct haplotypes with moderate genetic divergence, as indicated by a mean intraspecific divergence of 1.10% and a maximal distance of 1.87% (Tab. 1). This species is well known for its considerable geographic variation (Pitkin and Sattler 1991). Form “A” from the north-eastern part of the range (Austria, eastern Switzerland) is usually larger and more uniformly dark than specimens of form “B” from the south-western Alps (western Switzerland, Italy, France). Male genitalia of these two forms are similar (Figs 9–10, depicting specimens from France and Austria respectively), though Pitkin and Sattler (1991) found a tendency for the secondary vincular process to be slightly broader and directed laterally rather than posteriorly in form “A” compared with “B”. Furthermore, the females of both forms seem to differ slightly in genitalia. Resolution of their taxonomic status is complicated by the presence of intermediate forms. Sequence variation at COI is at least partially correlated with the distribution of morphological variation, as it separates western alpine populations and those from the Abruzzi Mountains from those of the north-eastern Alps (Fig. 36). Within both lineages divergence is comparatively high with >1% distance between Central Italy, south-eastern Switzerland and the south-western Alps or 1.4% divergence between a single specimens barcoded from Salzburg and others from Vorarlberg (Austria). Genetic variability was even considerable within single populations as four voucher specimens from Marguareis (Dep. Alpes-Maritimes, France) showed a maximum distance of 0.62%. *S. styriaca* also showed high intraspecific genetic divergence (2.34%) with no morphological differentiation. This species has a range that extends along the limestone ridge of the north-eastern-Alps of Austria similar to that of other north-eastern alpine endemics (Huemer 1998). In contrast the distribution area of a highly isolated population in the south-eastern Alps (Zirbitzkogel, Styria, Austria) is well known for differences in endemism compared with the North. Further examples probably reflecting persistent glacial isolation in this part of the Alps include e.g. *Colostygia austriacaria gremmingeri* Schawerda, 1942 (Geometridae) and *Elophos zirbitzensis* (Pieszczyk, 1902) (Geometridae) (Huemer 2009). Similarly elevated intraspecific genetic divergences without correlated morphological differentiation have been interpreted in the high alpine genus *Sciadia* (Geometridae) as reflecting increased nucleotide substitutions in response to the stress of high alpine habitat isolation (Huemer and Hausmann 2009).

Similar to many other alpine organisms, the evolution of *Sattleria* was strongly influenced by the cyclic change of colder and warmer periods during the Pleistocene (Haubrich and Schmitt 2007, Varga and Schmitt 2008). Whereas widely distributed arctic-alpine species, e.g. *Zygaena exulans* (Hohenwarth, 1792), probably survived glaciation in glacial steppes, particularly between the ice shields in the North and the mountains of the South (Schmitt and Hewitt 2004), species of *Sattleria* probably had more disjunct distribution patterns with increasing isolation and differentiation provoked by the early quaternary climatic crisis. Similar disjunct distributions are known in several alpine Lepidoptera with high mobility and no wing reduction in either sex, e.g. in the genus *Erebia* (Schmitt *et al.* 2006, Sonderegger 2005). Different refugia may have been a consequence and have to be considered for each taxonomic lineage. A somewhat similar diversification pattern occurs in the high alpine, brachypterous genus *Sphaleroptera* (Whitebread 2007) as it includes several partially sympatric taxa showing high interspecific divergence at COI (P. Huemer, pers. obs.).

While the timing of diversification in *Sattleria* remains uncertain, the congruent phylogeographic patterns in other Lepidoptera (e.g. *Erebia*, *Melitaea*) clearly indicate the role of climatic oscillations during the Quaternary on population isolation and differentiation (Albre *et al.* 2008, Leneveu *et al.* 2009). Estimations of average substitution rates for COI indicate that divergences of 1.0–2.5% correspond to divergence times of roughly one million

years (Hausmann *et al.* 2011, Kandul *et al.* 2004). Accordingly, the major lineages of *Sattleria* likely diversified from 1–6 mya (see Table 2). However, possible variation in substitution rates, and the likely presence of sequence variation at the onset of the Pleistocene adds uncertainty to this estimate. It seems likely that first divergence of *Sattleria* began in the lower Pliocene (5.3 mya–1.8 mya), and was reinforced by climatic oscillations in the late Pliocene and during the Pleistocene. The evidence for regional sequence variation in *S. melaleucella* suggests that populations of this species survived glaciation *in situ* in the Alps (and Apennines) leading to a remarkable genetic differentiation. Similar patterns have been detected in other alpine organisms, including endemic plants (Tribsch *et al.* 2002, Schönswetter *et al.* 2003) and Lepidoptera (Huemer and Hausmann 2009). The gene flow between populations of *S. melaleucella* was probably only partially interrupted by interglacial or postglacial disjunctions to higher mountain systems leading to several geographically separated haplotypes within this widespread species. The separation of southern alpine populations of *Sattleria* from a common ancestor most likely was driven by the climatically induced disjunction of populations found in unglaciated massifs near the southern border of the Alps. Female brachyptery and flightlessness combined with isolation of these mountain systems strongly reduced dispersal, and thereby disrupted gene flow. Differentiation centres persisted in the foothills of these mountains throughout the Pleistocene and populations simply shifted their elevational range in response to climate change, avoiding the need for long distance re-colonization (Schmitt 2007). The warmer temperatures in the southern Alps may have reduced generation times, producing higher divergence values, whereas populations of *S. melaleucella* in the Central and northern Alps likely encountered less favourable conditions, reducing the number of generations and levels of divergence. However, the sympatric occurrence of local endemics together with widespread species (*S. melaleucella* and *S. pyrenaica*) likely reflects the re-colonization of the shared habitat by one or both species over short distances or by the occupancy of different ecological niches. For example, the species pair *S. marguareisi* and *S. melaleucella* probably consume different host-plants (Huemer and Sattler 1992). The future expansion of molecular data sets to include data for nuclear genes will be crucial in the resolution of the numerous questions that are currently unresolved.

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